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THE EVOLUTION AND USE OF THE AFTERSHAFT IN BIRDS.

BY HUBERT LYMAN CLARK, PITTSBURGH, PA.

THE presence of an aftershaft on the contour-feathers of the body has long been recognized as a taxonomic character of some value in the classification of birds, but little, if anything, has been published regarding its history or use. Admitting that every part of the body either has some function, the exercise of which has tended to preserve and strengthen it, or else that, if functionless, it is gradually being atrophied, it is necessary, before the evolution of any organ can be followed through all its stages, to first discover if it has any function, and, if so, what it is. The probable history of the aftershaft can best be traced in this way, and so the first point to be settled is the question of its use. The primary function of feathers is the retaining of heat, and, while forming a non-conducting covering, it is still essential that the weight be as little as possible. As the feathers differentiated other functions, some becoming long and stiff for flight and steering and some taking on new shapes and colors simply for ornament, every change which made the coat of contour-feathers more compact was a distinct gain to the bird. If any feather with a well-developed aftershaft be examined, it will be seen that the smaller shaft lies exactly underneath the larger and its vanes are closely appressed to those of the main feather, thus practically doubling its thickness and increasing its heat-retaining power with the least possible loss of compactness. Now, on the other hand, if a feather is examined which has only a very small aftershaft, the latter is not closely appressed to the main shaft and adds almost nothing to its thickness or warmth. Exceptions will, of course, be easily found to these rules, but the fact remains that where the aftershaft is vigorous it gives plain evidence of adding warmth to the plumage, while it is clear that it can have no secondary function of ornament or locomotion. Another reason for believing that the aftershaft is functionally of no importance, except when an assistance to greater warmth, is found by examining the list of birds which lack it. They are as follows:—

1. Some Ratitæ (Ostriches, Rheas, Apteryx?).
2. Diomedinæ (Albatrosses).
3. Steganopodes (Gannets, Pelicans, Cormorants, etc.).
4. Lamellirostres (Ducks, Swans, Geese), except Flamingoes and some Ducks.
5. Columbæ (Pigeons).
6. Cathartidæ (American Vultures).
7. Striges (Owls).
8. Pandionidæ (Ospreys).
9. Cuculidæ (Cuckoos).
10. Alcedinidæ (Kingfishers).

Since there are known to science to day about ten thousand species of birds, only one-tenth of which are included in the above list, the absence of an aftershaft may certainly be considered exceptional. If it is functionally of any importance, why should it be wanting in the albatross, though present in the petrel? Or wanting in many ducks and present in others? And indeed to assign it any function common to all birds except to those in the above list, while wanting in all of them, will be readily found impossible. That it may be the cause of greater warmth receives a proof of negative value from our knowledge that, while very large in all the other Ratitæ, it is totally wanting in those species which inhabit the open plains and deserts of the tropics, where it is not desirable to retain too much heat. Still further evidence appears in the facts that all of the birds which lack an aftershaft (except owls and pigeons) are supplied with a thick coat of down beneath the contour-feathers, and all of the groups except Striges, Lamellirostres, and a few Steganopodes are most largely represented in the tropics and warmer temperate countries. While much of this evidence is very general, some of it purely negative, it seems undoubtedly true that the aftershaft, when not serving as an additional heat-retainer, is wholly functionless.

The conclusion is now unavoidable that the aftershaft, if functionless, must, according to our original proposition, be undergoing a process of gradual atrophy. That such is the case admits of little doubt. It must, however, be kept in mind that its possible function as a heat-retainer is admitted, and in cases where this function has been sufficiently exercised, atrophy, if ever begun, has been stopped. Illustrations of this may be found all through the class, but two will be sufficient to show the point. In the Casuaridæ (Cassowaries) the aftershaft is of equal size with the main shaft, and its function is undoubtedly the same. It is practically a second feather, and, since compactness of plumage is of no advantage to non-flying birds, it has continued to exercise its function, and atrophy has never begun. In the Gallinæ, one of the oldest and most generalized groups, where compactness of plumage is very desirable, not only because it creates less friction in flight, but also because, being essentially ground birds, they are greatly exposed to cold and damp, the aftershaft is large and thick, but entirely different from the Cassowary's. Increasing compactness of the plumage has greatly modified it, but atrophy has not occurred because it still exercises to an important degree its function as a heat-retainer. In the Passeres, on the other hand, the condition of the aftershaft shows evident loss of function and consequent atrophy, being very small and weak. Perhaps in no better way can the degeneration of the aftershaft consequent on its loss of function be proven than by an examination of the feathers of the wing. As is well known, the chief function of the primaries and secondaries is no longer heat-retaining but locomotive, and they entirely lack an aftershaft in all flying birds. But this change of function has undoubtedly been brought about gradually, and on the elbow of the wing are several feathers, very slightly different from the contour-feathers, which grade by almost imperceptible differences into the fully-developed secondaries. If these feathers are examined in any bird with aftershafted plumage, as, for example, the ruffed grouse (Bonasa umbellus), a very evident aftershaft will be found on the smallest ones, but decreasing rapidly in size as the main shafts become flight-feathers, until, on the true secondaries, they are either wholly wanting or represented only by a slight meeting of the vanes.

It will be noticed that throughout the preceding argument, the assumption has been made that the aftershaft is a degenerated and not a recently evolved part of the feather. That is, that it was originally characteristic of feathers in general and its condition as known to us is worse than formerly, rather than that it is an acquired character, which never occurred where it is now wanting. The truth of this assumption must now be proven, or the foregoing statements are meaningless. The first reason to be offered for believing it to be a primitive part of the feather is found in the facts of its occurrence and development in the different orders of birds. In the Casuaridæ, which is admitted to be one of the very oldest families of modern birds, we find a very large aftershaft, indeed, as already said, it is practically one-half of the feather. In the other Ratitæ, in which it is wholly wanting, local causes, such as excessive heat, have destroyed its usefulness, and its loss is easily explained. Large aftershafts are also found in Opisthocomus, the Gallinæ, and the Penquins, all old and little specialized groups; while, on the other hand, in the

most highly organized birds, as the Passeres, the aftershaft is very weak, and in many peculiarly specialized birds, as the owls, American vultures, ospreys, and kingfishers, it is wholly wanting. The second reason for considering it primitive is the process of its development during the formation of the feather. It is needless to republish here the history of a feather's growth, but it may be well to call attention to one or two points. When the malpighian layer covers the feather-papilla, it would naturally be thinnest on the sides. The increased thickness above and below would cause greater pressure on the papilla along the median line on both surfaces, thus causing the grooves in which the rhachis and hyporhachis subsequently develop. Now, it is known that both these grooves occur in those feathers which have an aftershaft, and it is much more probable that, though now the upper groove is the larger, they were originally of equal size, than that the lower groove is a secondary development; because it is difficult to assign any possible reason for its ever beginning at all as a secondary characteristic. The foregoing facts give warrant to the following theory of the evolution and subsequent degeneration of the aftershaft.

Paleontology shows us that flight was an accomplished fact long before birds were evolved, and, since it requires tremendous muscular energy, it would be an obvious advantage to the hypothetical avian ancestor to decrease his weight and, at the same time, increase the non-conductability of his covering. When, therefore, feathers were first evolved from scales, the object in view was increase of heat-retaining power combined with decrease of weight. The most natural way of improving scales in this direction would be to make them thicker and, at the same time, hollow, and continued development along this line would result in making them more or less quill like. Then by dividing longitudinally and at right-angles to the axis of the body the number would be doubled without taking up any more space on the body, an obvious advantage. Constant subdivision, making them more adjustible, more coherent, and more compact, would finally bring about a condition very similar to that of the down-feathers of many birds especially in the first plumage. From this condition it is not difficult to trace the gradual development into a contour-feather in which shaft and aftershaft are of equal size, such a condition, in fact, as we find in the Cassowaries. But in this condition the feathers cause far too great friction with the air to admit of rapid flight, and so there came about the natural evolution of the more coherent, pennaceous feather with its comparatively smooth surface. But the natural curve of the lower half of this primitive feather was up and outwards and in direct antagonism to the down and inward curve of the main shaft, and so, being a hindrance to the required compactness, it gradually gave way and degenerated to its present condition. The rest of the story has already been told; how, where the aftershaft has adapted itself to its sole function as heat-retainer, it is still strong and useful, but in all other cases it is either wholly lost or on the rapid road thereto. Whether subsequent investigations and discoveries in paleontology and histology confirm this theory remains to be seen, but, for the present, it is at least plausible and open to few objections.

BRITISH STONE CIRCLES.[1]

BY A. L. LEWIS, LONDON, ENGLAND.

No. 1. — Abury.

THE largest circle of stones in the world was that of which the remains — few when compared with the magnitude of the structure of which they formed part, but by no means inconsiderable in themselves — are to be seen at Abury, in Wiltshire. Abury village is six miles from Marlborough station (Great Western Railway); it occupies the site of the circles and is mainly built of fragments of the stones which composed them. The monument when complete consisted of a circle of one hundred stones (more or less), of which thirteen still remain above ground and at least sixteen more are buried, some of these are of great size, more bulky than any at Stonehenge, but unshaped and without the cross-pieces which distinguish the latter monument from all other circles. The diameter of this circle was about eleven hundred feet, or eleven times that of the outer circle at Stonehenge; inside it were two other circles,— north and south, — both over three hundred feet in diameter. Dr. Stukeley considered that there was a smaller circle inside each of these, but there is now nothing remaining of them, and it has been doubted whether they ever existed. In the centre of the northern inner circle there were three very large upright stones, forming a "cove" or three sides of a square, of which the open side was toward the northeast, and of these stones two still remain, besides which there are now only three stones of the northern inner circle or circles and five of the southern, and a single stone, which Stukeley said stood in the middle of the latter, has long since disappeared. The total number of stones composing the inner circles, "cove," etc., was, according to Stukeley, eighty-nine.

The circles (and the greater part of the village) are surrounded by a deep ditch, outside which is a high embankment. Aubrey, the first writer who noticed this monument, made a very imperfect plan of it in 1663, in which he represented an avenue of stones leading down in a straight line to the present main road, near the River Kennet, and another avenue of stones leading from the end of it, also in a straight line, but at a right-angle, to a smaller circle on Overton Hill, near the line of large barrows which crosses the main road from Marlborough before it reaches the point where the road to Avebury leaves it. Stukeley delineated these as one avenue running in a curved line about a mile long between the great circles at Abury and the smaller one on Overton Hill, and thought that it represented a serpent, of which the Overton Hill circle formed the head, and the Abury circles some convolutions of the body, the tail being represented by another avenue, which left the great circles near where the church now stands, and curved away to the left, passing two large stones called the "long stones," which are still to be seen,[2] though of the rest of the alleged second avenue nothing remains *in situ*, so that some archæologists think it never existed, especially as Aubrey, who visited the circles more than fifty years before Stukeley, has not left any notice of it. Stukeley, however, spent much more time at Abury than Aubrey did, and obtained much information from the inhabitants as to the former position of stones which had been destroyed within their remembrance, and, as there is much stone used in causeways, etc., over the marshy ground on that side of Abury, it is probable that an avenue of some sort did formerly exist there, but this a point for the visitor to investigate for himself.

The circle on Overton Hill and the end of the avenue adjoining it were destroyed before Stukeley went to Abury, but there are several stones of the other part of the avenue standing and fallen by the side of the road which leads from the main road at West Kennet to Abury village, and in a meadow under the left-hand hedge of the main road there are four fallen stones of the avenue, and, as these follow the curve which the road makes between the barrows and the turn to Abury, they seem to show that Stukeley was right in delineating a single curved avenue in place of the two, meeting at right angles, which Aubrey shows in his plan. This is another point for the visitor to verify, and he will do well to follow the avenue from these four stones to its junction with the circles at Abury, and, having inspected the latter, to go out past the church to the "long stones," and to the Beekhampton Inn, which is on the main road by which he will return to Marlborough, stopping on his way to climb Silbury Hill, the largest artificial mound in Europe. This attracts attention by its regular shape and flattened top, and, as it is due south from the circles at Abury, probably formed part of the monument; it has been dug into, but nothing has been found to show it to be a sepulchral mound, like the smaller barrows which are so numerous in this district. Human remains were found round the Overton circle, but none are known to have been found at Abury, so that it does not appear that the object of these circles was, as some suppose,

[1] It has been thought that many Americans who, when in England, visit Stonehenge may not be aware how many remains of a similar character, which they might also wish to inspect, exist in the British Isles; and the editor of *Science* has accordingly made arrangements for a series of short articles, which shall give a description of each of the principal circles and state what points should be noted and how it may most easily be visited.

[2] These are probably the last survivors of another large circle.